PLATE 11.

FIG. 4 and 5.—The two hammer-stones found in association with the Selsey rostrate. Drawn of the actual size of the specimens. That shown in the upper figure (fig. 5) is less than half the bulk of the other. It is of pyramidal form, and is drawn so as to show the apex of the pyramid as the centre of the picture, with three large concave flake scars and a fourth convex area, radiating from it. The apex shows numerous small fractures due to its use as the striking surface. The larger hammer-stone drawn in the lower figure (fig. 6) has also been shaped by large flakes to a pyramidal form. In this drawing the apex forms the top of the figure, the stone resting on the opposite surface or base.

# *Reversal of Asymmetry in the Plutei of* Echinus miliaris.

By HIROSHI OHSHIMA, Kyushiu Imperial University, Fukuoka, Japan.

(Communicated by Prof. E. W. MacBride, F.R.S. Received February 15, 1921.)

While engaged in artificial rearing of *Echinus miliaris* under the guidance of Prof. MacBride,* I have come across a number of abnormal plutei which had the hydrocœle developed on the right side instead of in its normal position on the left side. Such reversed larvæ were first found on May 31, 1920, when they were eleven days old (text-fig. 1). The "larval" body was quite normal both in size and shape, but the hydrocœle, stone-canal, axial sinus, madreporic vesicle, and amniotic invagination were all situated on the right side, so that the larva became a perfect mirror-image of the normal larva. Such larvæ developed further with exactly the same rate of growth as the normal ones, an echinus-rudiment being well developed on the right side, until at last, when a month old, some few of them passed metamorphosis. The young urchins (text-fig. 2) showed no features visible externally which differed from those of urchins metamorphosed from normal larvæ. A similar case has previously been described only by Runnström in two individuals found among artificially reared larvæ of *Strongylocentrotus lividus* ((9), pp. 2–3, 7–10; (12), pp. 419–24, Plate 14, figs. 12–16). In other classes of Echinoderms, auriculariæ with the hydrocœle on the right side were noticed by Müller many years ago ((7), pp. 101, 109; Plate 5, fig. 1), and a similar state of affairs in two plutei of *Ophionotus hexactis* has recently been discovered by

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* It is my pleasant duty here to express my extreme indebtedness to Prof. E. W. MacBride for his kind supervision on the present work, and to Sir Sidney F. Harmer for permission to use the British Museum (Natural History) Library. A more detailed account of this work will be published elsewhere before long.

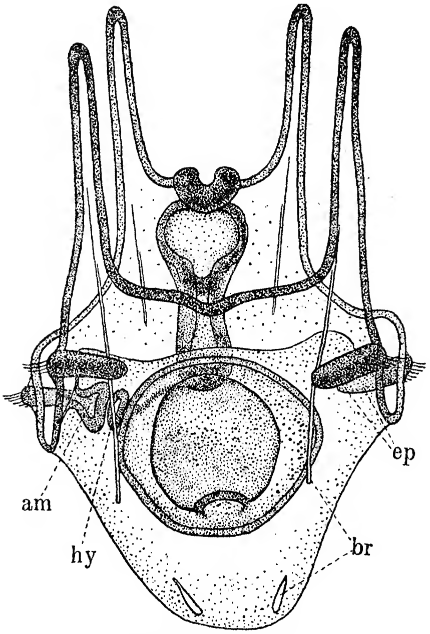

FIG. 1.—Ventral view of a reversed larva of *Echinus miliaris*, eleven days old; drawn from life. × 100. *am*, amniotic invagination; *br*, body-rod partly degenerated; *ep*, ciliary epaulettes; *hy*, hydrocœle.

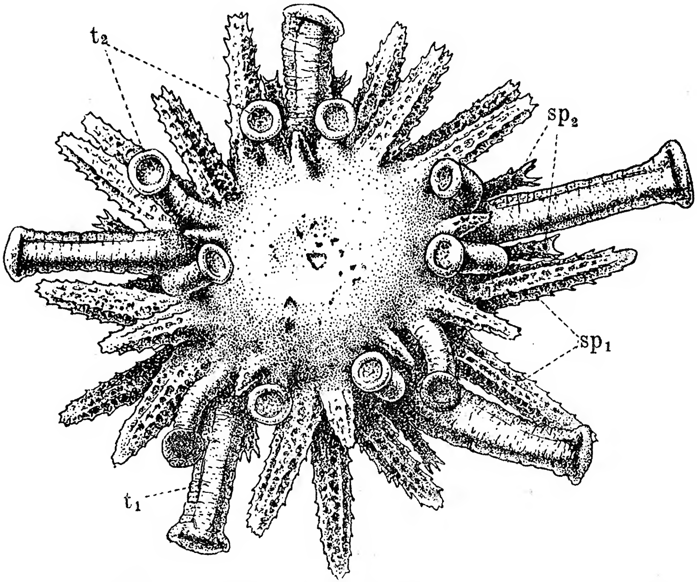

FIG. 2.—Young of *Echinus miliaris* metamorphosed from reversed larva, seen from actinal side; thirty-two days old, and shortly after metamorphosis; mouth not yet open; drawn from life. × 100. $sp_1$, thick pointed spines; $sp_2$, square-ending spines; $t_1$, primary tentacles; $t_2$, first paired tentacles.

Mortensen.* In both these cases the abnormal larvæ were found in nature, not reared under artificial conditions.

The purpose of our experiments was to repeat Prof. MacBride's method of artificial production of the double hydrocœle (6). Having been unable to get an uninterrupted supply of enough food, which consisted of *Nitzschia*, and from other causes unknown to us at present, we could not arrive at any satisfactory conclusion so far as the effect of the increased salinity is concerned. From both lots of cultures, treated with the "hypertonic" sea water as well as untreated, more than 10 per cent. of the larvæ exhibited the situs inversus, and much less number, 2 per cent. at most, developed the double hydrocœle.

There are at least three possible ways in which the situs inversus of the Echinoplutei may occur:—

1. It may be a case analogous to the reversed Gasteropods, as made known by Crampton and Conklin. Some unnatural conditions, unavoidable in the course of the artificial fertilisation of the sea-urchin eggs, may have changed the polarity of the latter, with the result that the structure of the larva assumes such a totally reversed situs (Conklin, (1), p. 585). It may be stated here in this connection that the phenomenon can hardly be regarded as due to heredity. Our cultures were obtained from three different parents. It seems highly improbable that we should find at least three congenitally reversed individuals (more than 4 per cent.) out of seventy sea-urchins which had been sent from Plymouth, and those three, those selected at random for their good eggs. The remainder were not tested. If the peculiarity were congenital, the occurrence of such reversed larvæ in nature would not be very rare.

2. Results of Runnström's experiments carried out with *Strongylocentrotus* and *Solaster* ((10), pp. 533–44, text-figs. 7*a*, 10; (14), pp. 471–73, text-figs. 16*a*, *b*) show that the larva developed from the right half of the egg or embryo of these Echinoderms had an indication of being a mirror-image of the normal form. If we compare this fact with Spemann's experiments on the twins and double monsters of *Triton*, in which the situs inversus occurred in most of the right side member ((15), pp. 390–93), we are led to suppose that the abnormal larvæ before us may have developed from those eggs or embryos which had accidentally undergone dissociation. Our abnormal larvæ were, however, neither smaller in size nor slower in development than the normal ones, so that the above supposition seems hardly

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* I have to acknowledge my hearty thanks to Dr. Th. Mortensen, who informed me of this discovery and kindly permitted me to mention it here.

acceptable in this case. On the other hand, we see in Gemmill's twin larvæ of *Luidia* ((2), Plate 2, fig. 13; Plate 3, figs. 19, 21) no indication whatever of a mirror-image on the part of the right side member. Thus, if it be true that the long-continued shaking caused the partial dissociation of blastomeres, as he interpreted the twin-formation, and in which interpretation there is room for some doubt, the result differs entirely from Runnström's.

3. The growth of a normally developing hydrocœle might have been arrested from some cause, and the right anterior cœlom, to compensate this defective development, produced a new hydrocœle on the right side. This seems to me most probable, if not exclusive, to have occurred in our case of abnormality, and it needs some further consideration.

From looking through the literature of the abnormal Echinoplutei and from my own observations, the following facts seem to me to have some important bearings on the formation of the abnormality in question:—

(*a*) Obliteration of the pore-canal (five cases in *Strongylocentrotus lividus* by Runnström, (9), p. 8; (12), p. 422; (9), p. 3; (12), p. 417, Plate 13, fig. 8*a*; (12), p. 413, Plate 13, fig. 4; (12), p. 415, Plate 13, fig. 5; (12), pp. 415–16. Two cases in *Echinus miliaris* by the writer, Culture No. 9, "treated"). This seems to happen in connection with the shifting of the pore towards the mid-dorsal line from its original position on the left side. The hydrocœle, thus deprived of its communication with the exterior, becomes arrested in its development, and then begins to degenerate quickly.

(*b*) Activation of the right anterior cœlom in its latent potentialities of producing a hydrocœle, to compensate the degenerating left hydrocœle. This new structure develops exactly after the manner of the normal hydrocœle on the left side. Actual observations of early stages of its formation are, however, unfortunately lacking.

(*c*) Restoration to the left hydrocœle of its external communication. This can take place either from the formation of a new pore-canal (two cases in *Strongylocentrotus lividus* by Runnström, (9), p. 8; (12), p. 422, Plate 14, fig. 15; (12), p. 416, Plate 13, figs. 7*a*, *b*), or from fusion of the left and right anterior cœloms into a single axial sinus (two cases in *Echinus miliaris* by MacBride, (6), p. 347, Plate 5, fig. 9; pp. 338, 348, Plate 8, fig. 18). The left hydrocœle will now continue to develop and differentiate further.

(*d*) Formation of an amniotic invagination on the right side. According to MacBride, this is due to the stimulating action of the right hydrocœle ((5), pp. 240–41; (6), p. 343), while Runnström is of the opinion that the invagination can be formed independently of the presense of a hydrocœle, though further development of both these structures are mutually dependent ((10), p. 305 ; (12), pp. 9–11, 13–14).

(*e*) Peculiar differentiation of the right posterior cœlom, to share with the hydrocœle and amniotic invagination in the formation of an echinus-rudiment, exactly as its left side fellow normally does.

(*f*) Formation of pedicellariæ on the left side. This occurs in the reversed larvæ (two cases in *Strongylocentrotus lividus* by Runnström (9), p. 2, (9), p. 10, (12), p. 422) and in some double-hydrocœle ones (*Echinus miliaris* MacBride (6), p. 343). They probably owe their existence to the echinus-rudiment developed on the opposite side. In the complete absence of hydrocœle from both sides pedicellariæ cannot usually be formed at all (exceptional cases are recorded by Runnström (11), pp. 269–70, text-figs. 33–35).

From these data above enumerated, if adequately combined, the following changes seem to be possible :—

Let us start with a young normal larva, in which hydrocœle, axial sinus, pore-canal, and dorsal pore are all formed on the left side. An amniotic invagination may already be formed on the left side, and the right anterior cœlom may be provided with a pore-canal.

Now, the dorsal pore of the left side happens to become obliterated, and is hence followed by the arrest of development of the hydrocœle and its subsequent degeneration. Two courses are here open :—

A. The right anterior cœlom begins to exhibit its unusual activity in producing a right hydrocœle, which acquires through a pore-canal a communication with the exterior.

B. The right anterior cœlom does not become active (presumably from want of sufficient nutrition). The result is the complete absence of hydrocœle from both sides.

The further fate of larvæ in which the course of events has been that indicated by A will be one of the following three :—

1. Appearance of a new dorsal pore on the left side, so that the left hydrocœle regains the power to develop further. If well fed, the hydrocœle on each side will continue to develop side by side, so as to give rise to a double-hydrocœle larva.

2. Fusion of the anterior cœloms of both sides takes place, so as to enable the left hydrocœle to communicate with the exterior and to continue further development. The result is also a double hydrocœle.

3. No reappearance of a second dorsal pore on the left side nor fusion of the anterior cœloms takes place. The left water-vascular system will consequently degenerate quickly, while the right one will develop like the normal left. *A larva with the situs inversus is the result.*

In both the courses of events indicated by 1 and 2 the following three conditions may possibly arise, according to the different stages at which the right hydrocœle had arrived, when the recovery of the left hydrocœle took place:—

(*a*) The recovery of the left hydrocœle takes place before the right hydrocœle attains a size equal to that of the left. The period during which the hydrocœle is deprived of communication with the exterior is very short. Under such a condition the larva in which the left hydrocœle is more advanced than the right will result. This is very frequently met with among double hydrocœle larvæ.

(*b*) The left hydrocœle recovers at the time when the right one has attained the size about equal to it. The larvæ developed under such a condition has two hydrocœles equal in their states of development. Such a case is less frequently met with than the former.

(*c*) The left hydrocele recovers late when the right one is already in a more advanced state than it. The period during which the hydrocœle is deprived of communication with the exterior is here very long. The result is that the larva has the left hydrocœle less developed than the right. Usually the hydrocœle cannot remain unchanged for so long a time after being deprived of its external communication. The case is therefore met with very rarely.

The above may not be the only ways of reaching the respective results, but probably are the commonest. Many modifications are naturally conceivable.

Whether the extraordinary development of a hydrocœle from the right anterior cœlom is to be regarded as a case of atavism or as other variation is, from the poor state of our knowledge at present, a matter of choice. MacBride ((5), pp. 240, 244; (6), pp. 341–45) and v. Ubisch ((16), pp. 444–45) are of the opinion that it is a case of atavism. Grave ((4), p. 43) made the objection to this view that it necessitates the admission of such an improbable fact that the Echinoderm ancestor had a double set of spines and dental apparatus. According to MacBride, the appearance of the right hydrocœle to a certain stage of development is an atavistic feature, but later the formation of the amniotic invagination and those calcareous structures is due to the action of a hormone emanated from the hydrocœle ((5), pp. 247–48; (6), pp. 342–43). If this peculiar ability has been acquired by the left hydrocœle during the later period of Echinoid history, as suggested by v. Ubisch, then how could it be transmitted to the right hydrocele now?

Gemmill, discussing the causation of the double hydrocœle in starfish larvæ ((3), p. 72), introduces the idea of homœosis, which I prefer to the atavistic view. The difficulty of accepting the idea of homœosis in such a case, as maintained by Grave ((4), p. 45), can easily be overcome, because the development of the double hydrocœle is not a feature of adaptation to larval life, as he assumes it to be.

The unusual development of a hydrocœle on the right side when the left hydrocœle is arrested in its development resembles the well-known phenomenon in the regenerating claw of *Alpheus* (Przibram (8)). If the large claw of this crustacean is amputated, this will be replaced by a small claw, whilst the small claw on the other side, which has not been operated upon, will become a large claw. Przibram called this "compensatory hypertypy." Obviously these two cases are different in that (i), whereas in the Echinopluteus there is no trace of a right hydrocœle in normal condition, the small claw of *Alpheus* represents neither a rudimentary condition nor an early developmental stage, but is quite a functional organ; and that (ii), whereas the left hydrocœle of the Echinopluteus is arrested in its development during its very early stage, the large claw of *Alpheus* is removed after it has fully developed. With the sense widened to include these two cases, Przibram's term is desirable to be adopted here also.

The manner in which the situs inversus occurs in Echinoplutei resembles that found in the *Triton* larvæ, as produced artificially by Spemann ((15), p. 407). In both cases the abnormality starts with a "defective" development of a single organ—the gut in *Triton* and the hydrocœle in *Echinus*. There is, however, a difference between the two in the further courses in which other organs are affected. In *Triton* the other adjoining organs are simply displaced by that abnormal behaviour of the gut, while in *Echinus* a new hydrocœle appears on the right side, and a new set of calcareous structures, etc., are thereby induced to develop. The left hydrocœle can, if it regains its chance of further development, produce another echinus-rudiment, so as to give rise to a double-hydrocœle larva. Such a feature is very improbable to occur in the case of *Triton*.

My interpretation of the double-hydrocœle formation as described above cannot hold true in the case of starfish larvæ. Usually in the starfish larva the cœlomic vesicles on both sides fuse and communicate with each other at the anterior end, and the right dorsal pore, if present at first, gradually atrophies. Here in this case the obliteration of a dorsal pore has no influence upon the development and differentiation of the hydrocœle on the corresponding side. Under such different conditions I think that the occurrence among starfish larvæ of the situs inversus as is found in Echinoid larvæ will be extremely uncommon. Gemmill's interpretation as to the cause of the double-hydrocœle formation ((3), pp. 54-55) cannot, in its turn, hold true in the cases of the Echinoid and Ophiuroid larvæ, as was pointed out by

MacBride ((6), p. 326). One feature is, however, certainly common to the double-hydrocœle larvæ of these three classes of Echinoderms, namely, the temporary arrest of the growth of the left hydrocœle in an early stage, from some cause or other. And this occurs more frequently under artificial conditions than in nature.

What then is the external factor which causes the arrest of growth of the left hydrocœle in the Echinoid larvæ? It seems to me that the obliteration of the pore-canal is a direct cause of the arrest, and that obliteration of the canal is associated with the presence of too much diatom food and other micro-organisms in the culture jar, which arouses either mechanical or physiological disturbance in the normal development of the larva. The phenomenon in which the latent potentiality of producing a hydrocœle of the right anterior cœlom is provoked has been ingeniously compared by MacBride to artificial parthenogenesis ((6), p. 341). He thus regards the hypertonic sea water as one of the chief factors producing the double hydrocœle. This most interesting hypothesis is not as yet fully proved, and it is desirable that it should be set free from criticisms through further test.

### *Note by* Prof. E. W. MacBride, F.R.S.

My friend Dr. Ohshima and I agree in our fundamental explanation of the development of two hydrocœles in the larva of *Echinus miliaris.* We both attribute this phenomenon to a latent power in the right anterior cœlom developing a hydrocœle, a power which is normally inhibited by the development of the functional hydrocœle from the left anterior cœlom. This latent power of the right side, which is also manifested in the larvæ of Asteroidea and Ophiuroidea, I believe to be an indication that the common bilateral ancestor of the Echinodermata had, corresponding to the hydrocœle, a paired organ equally developed on both sides of the body, and that, whilst the organ on the left side became further developed until it grew to be the water-vascular system and its appendages, the organ on the right side dwindled and disappeared.

Dr. Ohshima does not accept this explanation, but prefers to explain the development of a right hydrocœle as "homœosis." I think this is really to substitute a word for an explanation. What is meant by homœosis? The word was coined by Bateson (1894) to signify the phenomenon which appears in the meristic repetition of seriate organs, viz., that a segment sometimes acquires the characters of a member of the series preceding or succeeding it. But this phenomenon is now more fully understood; it depends on the formation of tertiary organs—as we may call them—under the stress of formative stimuli. Thus the proto-vertebræ of the developing newt Necturus are at first all alike, but that particular one will develop into a sacral vertebra which happens to come in contact with the pelvic girdle—and this may occur at slightly different levels on the two sides of the animal. Unless the right and left anterior cœlomic sacs of Echinoderm larvæ had been originally alike in their potentialities, it is difficult to see how the powers of one could have been transferred to the other, as they do not form parts of a series.

In the paper which I communicated to the Society in 1918, I gave reasons for believing that one means of procuring the growth of two hydrocœles was to subject the growing larvæ to the action of hypertonic water for a period of about a week. This result was obtained during the summer of 1917. During the summer of 1919 I repeated the experiments, and obtained results so entirely confirmatory of those obtained in 1917 that I did not think it worth while to publish them.

During the spring and summer of 1920, when Dr. Ohshima worked in my laboratory, attempts to procure similar results failed: we did, indeed, obtain a few larvæ with double hydrocœles, but these were found mostly in cultures which had not been treated with hypertonic water at all.

Dr. Ohshima is naturally sceptical as to my diagnosis of the cause of the appearance of the double hydrocœle. I have therefore to offer the following suggestions as to the reason for the divergence of the results of 1920 from those of 1917:—

(1) The experiments of 1917 were carried out in natural sea water, which up till that time was sold—as in pre-War days by the Great Eastern Railway Company—at a cheap rate in London.

After the spring of 1917 this service was stopped, and for further experiments we had to rely on artificially prepared sea water, which is not so good for the growth of the larvæ.

(2) Dr. Ohshima's work is based on the results of two cultures, one obtained during May and one during June.

The May culture was not a very vigorous one—in other words, the proportion of ripe viable eggs shaken out was small compared to the mass of unripe eggs, and the early development was not very vigorous, though ultimately quite a considerable number of larvæ completed their metamorphoses.

I suggest that in the case of this culture the reaction to hypertonic water, which I noted in the vigorous culture of 1917 did not take place.

(3) On the other hand, the June culture was an extremely vigorous one. When I examined the larvæ of that portion of it which had been exposed to the action of hypertonic water, a large proportion showed signs of the

beginning of the development of a right hydrocœle. Then, however, in spite of all our endeavours to keep it alive, the Nitzschia culture, which was used for food, died off, and the development of the Echinus larvæ was consequently arrested. In fact, all of those that had been exposed to the action of hypertonic water died, and the larvæ in the control culture were given up for lost. But two months afterwards Dr. Ohshima, returning after an absence, found many of these larvæ alive and in an advanced state of development, and amongst them he discovered, in addition to a certain number of right-handed larvæ, a number which had developed two hydrocœles.

The explanation of this phenomenon which I suggest, is that the long period of starvation had checked the normal development of the left hydrocœle, so that this had remained small, and when conditions improved the innate tendency of the right side to develop a hydrocœle was no longer inhibited by too great a development on the left side.

If this explanation is justified in Dr. Ohshima's specimens, the right hydrocœle would have been produced by the *negative method* of checking the development of the left side, whilst in my earlier experiments it was produced by the *positive method* of direct stimulation of the right side.

Dr. Ohshima quotes an observation of Runnström's to the effect that a larva had been observed by him devoid entirely of a hydrocœle, but with pedicellariæ developed on both sides. I suggest that Runnström has overlooked the presence of vestigial hydrocœles in this larva. As I proved in 1918 (6), when larvæ are starved so that the hydrocœle rudiment is completely absorbed, they develop pointed spines on both sides, but no pedicellariæ. I too, like Runnström, imagined that I had found larvæ with pedicellariæ on both sides, but no hydrocœle; but these, when mounted whole and closely examined, disclosed minute hydrocœles on both sides.

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# *The Energy Involved in the Electric Change in Muscle and Nerve.*

By A. V. Hill, F.R.S.

(Received April 8, 1921.)

Considerable electromotive forces are produced by the activity of excited muscles or nerves—up to three or four hundredths of a volt—and it was conceivable that an appreciable amount of energy might be involved in the currents set up in the tissue by them. This paper contains an examination of the question.

In fig. 1 is shown a nerve fibre, on which rest electrodes (not shown) connected to an electrometer or galvanometer. Along the outside of the fibre is travelling, from right to left, a wave of negative potential, with velocity $a$ cm. per second, having at any point distant $x$ cm. along the nerve, and at time $t$ seconds, a value $y$ volts, as recorded on the electrometer, and shown (after the appropriate analysis) in the lower curve of the figure. We are not concerned here with the cause of this electromotive change, nor with what happens inside the fibre, but only with the physical results of it in an external circuit.

In consequence of the differences of potential existing along the length of the nerve, currents tend to flow, as shown by the full arrows and the strength of the current flowing at any moment between two neighbouring points, is